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The obligate fig-pollinator family Agaonidae in Germany (Hymenoptera, Chalcidoidea)

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Abstract

All native and many cultivated fig plants are pollinated by representatives of the family Agaonidae (fig wasps), which are specialised, secondarily phytophagous relatives of parasitoid wasps that evolved an obligate mutualism with fig trees. So far, distribution of Agaonidae in Europe has been limited to southern, mostly Mediterranean areas, for example, in Greece, Croatia, Hungary, Italy, France, Spain and Portugal. Here, we report the first four records of the family for Germany, all in the form of the widespread species *Blastophaga psenes* (Linnaeus, 1758). New verified records are from three States in western and south-western Germany, Baden-Wuerttemberg (Radolfzell at Lake Constance and Sasbach am Kaiserstuhl near Freiburg), Saarland (Saarbrücken) and Northrhine-Westalia (Bochum) and all are based on citizen-scientist observations and collections. The new records are considerably more northern than previously recorded localities and, strikingly, geographically distant from these. All records can be attributed to the presence of large male caprifig trees (*Ficus carica* L. var. *caprificus*), whose three generations of fruits host the development stages of *Blastophaga psenes*. We generated DNA barcode data of specimens from three localities and added them to the national GBOL (German Barcode of Life) database and the international Barcode of Life database (BOLD). The somewhat surprising occurrence of the species/family in Germany might be attributable to increasing temperatures as a result of global warming, but this needs further investigation. Additionally, the presence of fig wasps, assuming it stabilises, could offer new opportunities for fig farming in Germany.

Key Words

Fig wasps, *Ficus carica*, *Blastophaga psenes*, pollination, first records

Introduction

All species of the genus *Ficus* (figs) (Moraceae) depend on obligate pollinators of the wasp family Agaonidae (Hymenoptera, Chalcidoidea). There are about 880 accepted species of figs and many more undescribed (POWO 2023), associated with, so far, 640 described species of agaonid fig wasps, which represent probably about 20–30% of the existing species (van Noort and Rasplus 2023). Numerous additional chalcid wasp species complement the fig system as facultative pollinators, inquilines or parasitoids of other fig-associated wasps. Fig fruits are not only vital food sources in natural environments for many vertebrates and invertebrates, but also commercially important. The

† Deceased.

commercially most important species is *Ficus carica* L., which produces the well-known eatable fig fruits. More than 1,200 cultivars of *Ficus carica* are pomologically described (e.g. Condit (1955)). The yearly average worldwide fig production in 2015–2019 was 1,185,768 metric tonnes on 285,513 ha of cultivated area (Ferrara et al. 2022). The close association with fig plants and its striking diversity make Agaonidae a group of special ecological and economic relevance. In Europe, only few species are present. *Blastophaga psenes* (Linnaeus, 1758) is the most widespread, with populations limited to southern, mostly Mediterranean areas, for example, in Greece, Croatia, Hungary, Italy, France, Spain and Portugal. It has not been reported in Germany; the nearest validated records in France are hundreds of kilometres away from the German border (Baud 2008, 2023). Here, we report records of the fig wasp *Blastophaga psenes* from *Ficus carica* trees in four different localities across western and south-western Germany, these being the first records for the Agaonidae family in Germany. All recorded specimens were observed and collected by citizen scientists from the fig enthusiasts' community. Wasps were photographed, identified, DNA-barcoded and vouchered. *Blastophaga psenes* and *Ficus carica* are connected by a complex pollination and reproduction cycle. In order to discuss and understand the background of the records of *B. psenes* reported herein and to link the entomology and the fig community in this interdisciplinary paper, we provide an overview of this complex connection with a little more detail.

Ficus carica shows a special type of inflorescence called the syconium, which is built as a fleshy fruit from the stem (Stover et al. 2007). It is urn-shaped and contains multiple flowers, which can only be accessed through a small hole, called the ostiolum. *Ficus carica* is a gynodioecious, but functionally dioecious plant species (Kjellberg and Valdeyron 1990; Aradhya et al. 2010). The caprifig plants, also known as *Ficus carica* L. var. *caprificus*, have bisexual flowers with both fertile male flowers, which spend pollen, and sterile short-styled female flowers, also called gall flowers. They functionally represent the male plant. The function of the gall flowers is to host the eggs laid by *Blastophaga psenes* and then develop the pulpy gall and feed the fig wasp larvae. The fig plants sensu stricto, also known as *Ficus carica* L. var. *domestica* (Fruit Fig, Edible Fig) which bear the eatable fig fruits, are unisexual and have only fertile long-styled female flowers. They functionally represent the female plant. *Ficus carica* bears – depending on the cultivar – up to three generations of fruits every year. The first generation are the Profichi (male) and Breba (female), which start to grow in spring from the previous year's wood and buds. The second generation are the Mammoni (male) and Fichi (female), also called Main Crop, which start to develop in summer from the newly-grown wood and buds of the same year. Later in the year, male figs grow the Mamme as third generation fruits; these enable the overwintering of *Blastophaga psenes*.

Female fig cultivars are differentiated by their fruit generations into two types: Uniferous cultivars grow mainly Fichi and no or almost no Breba fruits. Biferous cultivars grow both Breba and Fichi. Female fig cultivars are also differentiated by their ability to grow parthenocarpic fruits (i.e. fruits without pollination). The Smyrna type only grows fruits with pollination. The Common type, sometimes also referred to as the Adriatic type, grows and ripens all fruit generations without pollination, though pollination can occur. The San Pedro type grows ripe Breba without pollination, but ripe Fichi only after pollination. Since *Blastophaga psenes* has, so far, not been present in wide areas of central and western Europe, including Germany, figs are almost exclusively grown as a hobby and not as a commercial fruit. Due to a large number of parthenocarpic Common and San Pedro cultivars, it is possible to grow figs without the pollinator. However, in the main production areas, the so-called caprification has been actively aided for centuries by planting caprifig trees or by hanging male caprifig branches in the fig plantations (Prgomet and Prgomet 2020; Kjellberg et al. 2022). Pollination from caprification results in less fruit dropping, in larger fruits, earlier ripening and also in a better taste. The sole pollinator of *Ficus carica* is *Blastophaga psenes*. After winter, the first generation of *B. psenes* develops in the gall flowers of the Mamme from the year before. The highly-modified wingless male wasps emerge first and inseminate the winged female wasps within the fig. The male wasps help the females to escape from the syconium by chewing narrow tunnels. The female wasps carry some of the omnipresent male pollen of the Mamme flower. The female wasps then reach the next fig trees by active or wind-driven flight and enter the figs through the ostiole (Kjellberg et al. 1987). In the case of a male syconium (Profichi or Mammoni, in the first or second generation, respectively), the wasp will successfully oviposit into the flowers and the next generation of fig wasps can develop in the gall flowers. In case of a female syconium (Breba or Fichi, in first or second generation, respectively), which includes only long-styled fertile female flowers, the wasps pollinate, but do not oviposit and then die and are digested, presumably by the specific enzyme Ficain. In the Mamme as the third generation of male syconium, *B. psenes* will overwinter.

Both species, *Ficus carica* and *Blastophaga psenes*, rely on a fine-tuned interaction with three fruit and wasp generations, with male and female figs and on perfect timing. The fig trees in central Europe, for example Germany, that are sometimes just ornamental plants, are usually parthenocarpic female trees. Previously, male fig trees were found only occasionally in Germany, but in recent years, their number has been growing (Rehberger 2023). Their presence is a prerequisite for the occurrence and establishment of fig wasps in Germany.

Methods

Institutional abbreviations

SMNS – Staatliches Museum für Naturkunde Stuttgart, Germany
ZFMK – Museum Koenig Bonn, Germany

ZSM – SNSB-Zoologische Staatssammlung München, Germany

Fig wasps were collected out of male fig tree fruits at different locations in Germany. They were either immersed in ethanol or died dry and were shipped to ZFMK for DNA barcoding or to ZSM for morphological identification.

DNA barcoding

At ZFMK, we processed 21 specimens from three locations in Baden-Württemberg (Radolfzell and Kaiserstuhl) and North Rhine-Westphalia (Bochum). We extracted DNA and amplified the CO1 barcode region at the molecular lab of the ZFMK following the protocols described in Jafari et al. (2023). Amplification and subsequent sequencing using forward primer LCO 2198-JJ and reverse primer HCO 2198-JJ (Astrin and Stüben 2008) did not yield any sequences. Alternatively, as forward primer, we used the newly-designed Heloridae-CV-F (primer sequence 5-TATTTGGAATATGAGCAGG-3) (published herein) and, as reverse primer, the HCO 2198-JJ primer. The amplified fragment is 619 bp long. Of the total of 21 specimens, 20 were successfully sequenced. In 18 of these, the barcodes fulfil all necessary criteria (e.g. chromatogram quality, ≤ 1% ambiguities or disagreements between the contig sequences) to meet the defined GBOL gold standard (see, for example, Jafari et al. (2023)). Accordingly, the sequencing success is 85.7% or 95.2% including the non-gold standard specimens. Sanger sequencing was done by BGI BIO Solutions Co, Ltd. (Hong Kong).

We complemented our sequences with one *Blastophaga psenes* sequence downloaded from BOLD (BOLD sequence ID: GBMIN30266-13) and outgroup sequences downloaded from BOLD (*Pleistodontes* sp., BOLD sequence ID: ASMII11091-22; *Blastophaga silvestriana*, ID: GBAH19865-19; *B. nipponica*, ID: GBAH20335-19; *B. yeni*, ID: GBAH20406-19). All sequences were aligned with the MUSCLE (v. 3.9.425) algorithm allowing for a maximum of eight iterations (Edgar 2004). For the sole purpose of alpha taxonomical evaluation of conspecificity, we calculated a Neighbour-Joining tree using the Tamura-Nei distance model (Tamura and Nei 1993). We added bootstrap support values, based on 325,235 seed value (Geneious default) and 1,000 replicates. The final tree is rooted with *Pleistodontes* sp. We performed all steps from alignment to tree reconstruction in Geneious Prime 2022.1.1 (Biomatters Ltd.). We uploaded all successfully produced barcode sequences to BOLD (Ratnasingham and Hebert 2007) to the dataset DS-DEBLPSEN; the respective BOLD-IDs are listed in Table 1.

Results

Confirmed records of *Blastophaga psenes* (those complemented by DNA barcodes marked *) in order of discovery date are:

1. Radolfzell*, found by Raphael Gebhard for the first time on 12.05.22 and also in 2023.
2. Saarbrücken, found by Anja Ruppert for the first time on 25.05.2022 and also multiple times in 2023.
3. Sasbach im Kaiserstuhl*, found by Stephan Rawer and Silvan Rehberger for the first time on 16.08.2022 and also in 2023.
4. Bochum*, found by Nikolaj Spiegel for the first time on 17.08.2022 and also multiple times in 2023.

Note that we do not give more detailed locality data to prevent vandalism of the respective fig trees. Detailed locality data are available from the authors upon reasonable request.

Localities are on display in Fig. 1. Vouchers are deposited at ZFMK, SMNS and ZSM (Table 1). In addition,

Table 1. BOLD-IDs of barcoded specimens, along with specimen IDs and depository information.

Specimen ID	Locality	Sex	BOLD-ID	bp-Length (ambiguities)	Depository
ZFMK-TIS-2637655	Bochum	♀	GBHYG1886-23	619(0)	SMNS
ZFMK-TIS-2637656	Bochum	♀	GBHYG1887-23	619(0)	ZSM
ZFMK-TIS-2637657	Bochum	♀	GBHYG1888-23	619(0)	ZFMK
ZFMK-TIS-2637658	Bochum	♀	GBHYG1889-23	619(0)	ZFMK
ZFMK-TIS-2637659	Bochum	♂	GBHYG1890-23	619(0)	ZFMK
ZFMK-TIS-2637660	Bochum	♂	GBHYG1891-23	619(0)	ZFMK
ZFMK-TIS-2637661	Bochum	♂	GBHYG1892-23	619(0)	ZFMK
ZFMK-TIS-2637662	Bochum	♂	GBHYG1893-23	619(0)	ZFMK
ZFMK-TIS-2637670	Sasbach/Kaiserstuhl	♀	GBHYG1894-23	619(0)	SMNS
ZFMK-TIS-2637671	Sasbach/Kaiserstuhl	♀	GBHYG1895-23	619(0)	ZSM
ZFMK-TIS-2637673	Sasbach/Kaiserstuhl	♂	GBHYG1896-23	619(0)	ZFMK
ZFMK-TIS-2637674	Sasbach/Kaiserstuhl	♂	GBHYG1897-23	619(0)	ZFMK
ZFMK-TIS-2637675	Radolfzell	♂	GBHYG1898-23	619(0)	SMNS
ZFMK-TIS-2637677	Radolfzell	♂	GBHYG1899-23	619(0)	ZSM
ZFMK-TIS-2637679	Radolfzell	♀	GBHYG1900-23	619(0)	ZFMK
ZFMK-TIS-2637680	Radolfzell	♀	GBHYG1901-23	619(0)	ZFMK
ZFMK-TIS-2637681	Radolfzell	♀	GBHYG1902-23	619(0)	ZFMK
ZFMK-TIS-2637682	Radolfzell	♀	GBHYG1903-23	619(0)	ZFMK

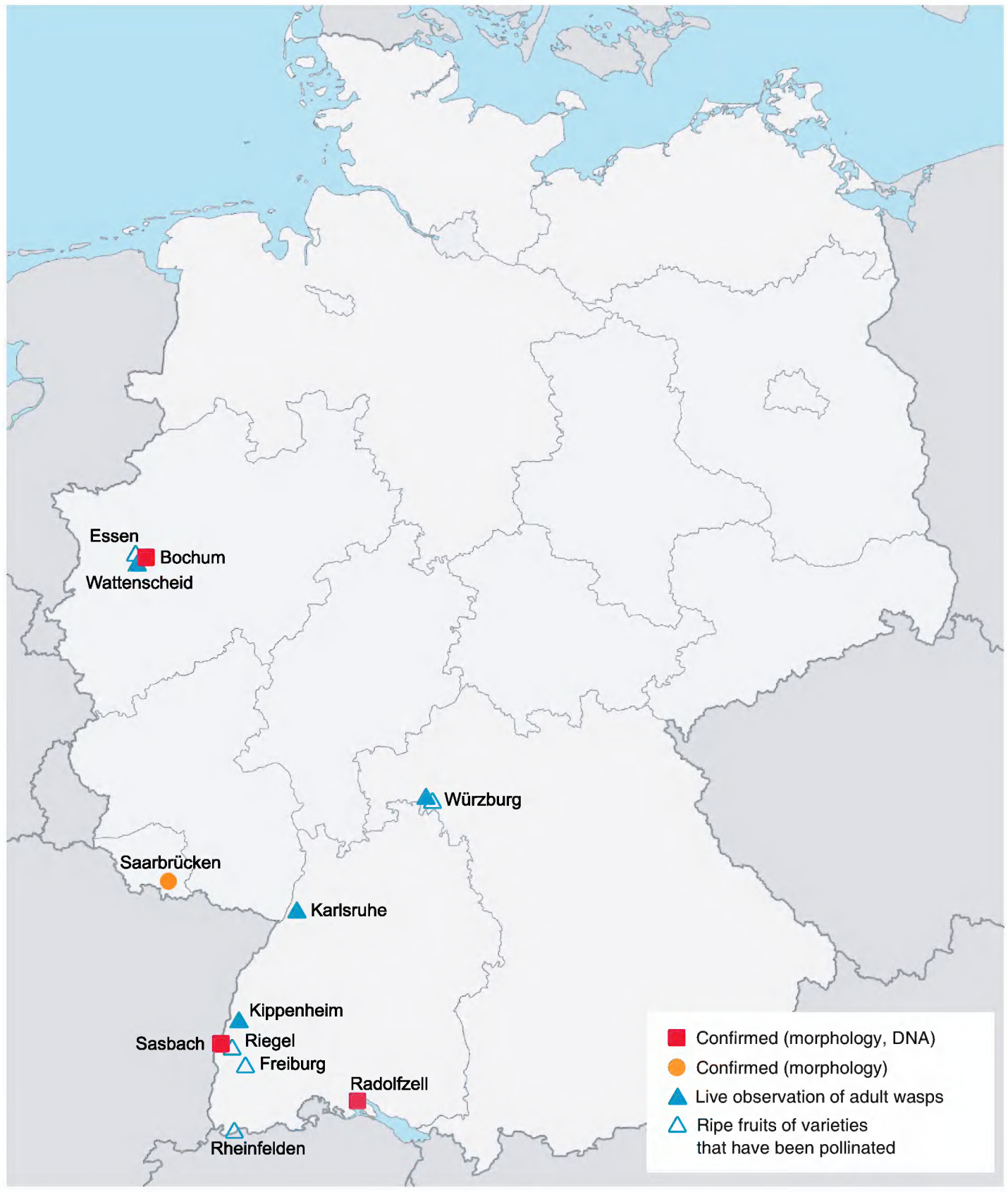

Figure 1. Map of records of *Blastophaga psenes* in Germany. Base Map Licence: CC BY-SA 3.0, Wikimedia Commons, Author: NordNordWest.

members of the *Ficus carica* Facebook group have recorded observations from 2023 of large numbers of fig wasps entering the ostiolum or emerging from caprifig fruits in Würzburg, Karlsruhe and Kippenheim near Offenburg. These observations lack detailed species identification and records are not vouchered. However, because of the uniqueness of the wasp and system reported here, we consider these records reliable and valuable and, ergo, also added them to Fig. 1, represented by blue filled triangles. Finally, pollinated Main Crop fruits from cultivars with obligatory pollination, indicating successful pollination, were observed in Riegel am Kaiserstuhl and Freiburg im Breisgau in 2022 and 2023, as well as in Wattenscheid, Essen and in Rheinfelden in 2023. These records do not include observed, identified or vouchered wasps, but are also shown in Fig. 1, represented by blue outlined triangles.

Analyses of DNA barcodes show conspecificity of the specimens with sequences generated herein, as well as with the *B. psenes* sequence added from BOLD, with a maximum intraspecific difference of 1.1%. There is a notable distance between the specimens from the Kaiserstuhl and the remaining specimens from Bochum and Radolfzell (Fig. 2). The barcode sequences between these two groups differ by 0.6–1.1%. Within the clusters, there is a maximum difference of 0.5%. Morphologically, all specimens from Germany we consider conspecific.

Discussion

The records of the agaonid *Blastophaga psenes* (Fig. 3) in Germany in 2022 came as a surprise, even more so since records are from four different, disjunct localities, ranging as far north as the City of Bochum in central-western Germany. These unexpected records immediately prompt the question as to why they are now present. Figs do not belong to the autochthonous flora of central Europe, but are considered as archaeophytes for Germany and have

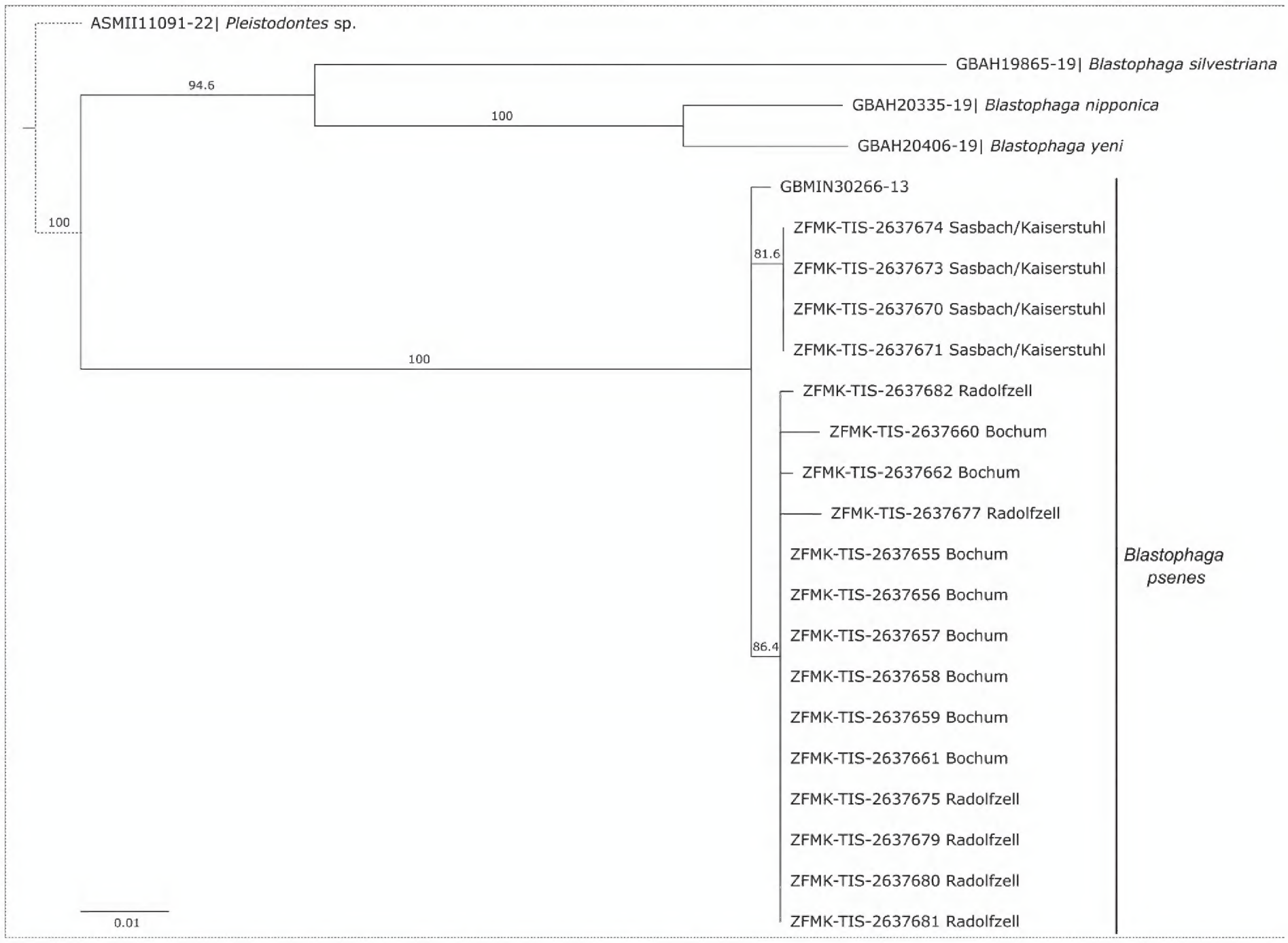

Figure 2. NJ tree, based on DNA barcode data for *B. psenes* specimens from three localities in Germany, complemented with one *B. psenes* sequence, three congeneric sequences and one *Pleistodontes* sp. (Agaonidae) sequence accessed via BOLD. The dotted branches that connect *Pleistodontes* sp. are not to scale. The support values (bootstrap with 1,000 replicates) are indicated on the respective branches.

been cultivated in Germany for more than 1,200 years (Gareis 1895; Knörzer 1981). Therefore, a long time has passed with figs present, but without any records of *B. psenes*, i.e. presumably without the species being present, in Germany. The nearest known reproducing populations of *B. psenes* are located in Provence (France), in Tuscany (Italy), in Croatia and in Hungary. In France, *B. psenes* is present only south of the line between Bordeaux and Lyon and only in non-mountainous areas (Baud 2008, 2023). Farmers in northern Italy have observed fig wasps occasionally in the lower warm parts of the valleys in the southern Alps in recent years, but not with stable reproducing populations (pers. comm. 2023). By linear distance, these could be the nearest populations, but the Alps are certainly a barrier for natural range extension of *B. psenes*. The other nearest populations are separated from the newly-recorded sites in Germany by 400 km (France) and 600 km (Hungary and Croatia). The intraspecific differences in DNA barcode sequence (i.e. a maximum of 1.1% between two groups; see results) might indicate that specimens from Kaiserstuhl and from Radolfzell/Bochum have different originating populations. It is possible that small populations were already present in Germany in previous years, but were overlooked. As outlined in the Introduction, successful reproduction of *B. psenes* depends on a complex chronological interplay with male and female fig trees and their fig fruit generations. All prerequisites must now be fulfilled at various locations in Germany, otherwise the records would not have been possible. Given the complexity of the system, it is unlikely that the records reported herein are the result of an immediate change, suddenly bridging hundreds of kilometres. Unpublished records of fig wasps from the fig hobbyists' community in Alsace (France), Gent (Belgium), The Hague (Netherlands), Graz and Klagenfurt (both Austria) from 2023 indicate a step-by-step change and spread from both western and eastern populations, presumably along the rivers Danube, Rhine and Rhône. It is a task for the future to compare the German populations with those from other regions of Europe in order to reconstruct the origins of range extensions.

Higher mean temperatures as a result of climate change are the first obvious explanation for the new records in Germany, as is well known for many other insect taxa – for example, the fig-associated lepidopteran *Choreutis nemorana* (Hübner, 1799) (de Prins et al. 2014). However, con-

Figure 3. *Blastophaga psenes* female (collected in Saarbrücken in 2022), displaying the unique habitus of agaonid wasps.

sidering the highly-specialised obligate mutualism with *Ficus carica*, increased temperature alone cannot explain the occurrence of *B. psenes* in Germany. A necessary, but not sufficient condition for *B. psenes* to reproduce is the presence of male caprifig trees with fruits at all stages of its range extension routes. In recent years, the occurrence of male caprifig trees has significantly increased in central Europe (Rehberger 2023). The plants grow wild along the banks of rivers and lakes, in harbours and adjacent to sewage channels, possibly from seeds distributed by birds or from remains of figs consumed by humans or they are – often unintentionally – cultivated in public parks and also private gardens by people taking wild trees or cuttings with them from their holidays, not knowing that they might not bear eatable fruit. Maybe these occurrences of male caprifig trees allowed both migration and establishment of new populations of *B. psenes*.

At the moment, we do not know whether or not these populations become established. However, since the 2022 generation of the wasps already was the result of a successful reproduction and since more occurrences were recorded in 2023, it is well possible that these populations will establish and even spread further. Statements have to be made with caution, because *B. psenes* has not been known to expand its range, but is known to be difficult to establish in new areas. One of the best known examples is the deliberate introduction of *B. psenes* in southern California for the purpose of cultivating Turkish Smyrna fig cultivars. After many failed attempts with other species of *Blastophaga* and also some failures with *B. psenes* they finally succeeded in 1889 (Eisen 1891; Ramirez 1970). After that, no range extension was observed and attempts for introduction in Texas, southern Arizona and Florida failed. In China, *B. psenes* has recently been considered for a local introduction and local domestication, as well as de-novo-domestication of wild pollinators via host-switches (Wang 2023). These activities show the importance of the pollinator for commercial fig production. Both yield and tasting quality of cultivated figs for some cultivars improve with the presence of the specialised pollinator. Cultivars of the Smyrna type fully depend on pollination by fig wasps. Hence, these new records will also be of economic interest because establishment of *B. psenes* in Germany and other regions of western and central Europe might enable future commercial fig farming.

Conclusion

The multiple records of this extraordinary wasp taxon Agaonidae in Germany are the starting point for more in-depth studies on the details of the extension of the species' range as well as on their potential to fundamentally change fig plant cultivation in central Europe. In our team of citizen and professional scientists, we will curiously monitor the development over the next years and continue to study the story of this intriguing plant-insect-interaction in Europe.

Acknowledgements

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